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## Putting assembly rules to work

Douma, J.C.

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## CHAPTER

# 6

### | General discussion and synthesis

## Traits can be used to predict vegetation distribution

The general aim of this thesis was to develop a trait-based vegetation model that predicts vegetation distribution based on functional relationships between the environment and the vegetation. The background for my research was that current vegetation models cannot be used with sufficient confidence for future projections of vegetation distribution because they either suffer from a lack of included ecological processes (correlative Habitat Distribution Models, HDMs) or from the practical impossibility to parameterize models for a large number of species (mechanistic vegetation models) (Chapter 1). I investigated whether plant traits can bring ecological realism to HDMs and as such bridge the gap between correlative vegetation distribution models and the mechanistic vegetation models.

Plant traits may bring this realism to HDMs, because they reflect how plants respond to environmental drivers. However, so far, plant traits have not been used in vegetation models and it is therefore not known to what extent they can be used to predict the vegetation distribution. To test this, I respectively investigated: 1) which traits are needed to optimally distinguish among plant communities from different habitats, 2) how these traits are related to environmental drivers and how they are modulated by other traits, 3) whether we are able to predict vegetation distribution once combining the knowledge of 1 and 2, and 4) the trait dynamics of plant communities during succession, as a first step towards a dynamic trait-based model.

Chapter 2-5 provided evidence that traits can indeed be used to predict the distribution of vegetation types and as such can be used to increase functionality in HDMs. However, the degree to which the distribution of vegetation types can be predicted successfully hinges on a number of issues. In the sections below, I present an integrated discussion of these critical success factors and the most important steps to be taken to improve the trait-based modelling approach.

## Traits provide a general and continuous link to environmental drivers

There is a growing body of evidence that environmental conditions constrain the number of viable plant strategies (see Introduction and Chapters 2-5 for references). As a result, species within the same habitat are on average functionally more similar than species of different habitats. This thesis builds on the insights of those studies to generate environment-trait relationships to predict traits from environmental drivers. Chapters 3 and 4 show that plant traits can be very well used to explain the occurrence of plant species by the environment, even though I used so called ‘soft traits’ (easy and quick to quantify; Cornelissen et al., 2003). Despite the fact that a large portion of the variability in traits can be explained by environmental drivers, further reducing the uncertainty in environment-trait relationships is urgently needed as these uncertainties propagate through the model and finally reduces the accuracy of with which the vegetation types are

predicted. Chapter 4 shows that the accuracy of the vegetation type predictions drops with 30% when using predicted trait-values instead of measured trait values, emphasizing the importance of correctly estimating traits from environmental drivers.

Environment-trait relationships can be improved on either side: by better estimates of environmental drivers or the selection of 'hard' traits that are better related to these drivers. In that respect, improving the estimates of nutrient availability deserves priority since the measures of nutrient availability had the lowest explanatory power of all the environmental drivers used (34%, or 48% when coupled to leaf economics traits; Chapter 3 and 4 respectively). The poor descriptive capacity of the nutrient availability indicators (both soil C/N ratio and soil C/P ratio as well as modelled nitrogen mineralisation) has been reported earlier (Ertsen et al., 1998, Ordoñez et al., 2009 and Ordoñez et al., 2010b). I think that the poor descriptive capacity of the nutrient availability indicators can to a large extent be explained by the fact that a substantial amount of the total nitrogen and total phosphorus (the measures are based on total nitrogen and phosphorus) are bound to soil particles or stored in recalcitrant litter (Aerts and Chapin, 2000) and thus will slowly (or not at all) become available for plants. Also, it would be better to measure nitrogen mineralisation throughout the year (instead of the modelled nitrogen mineralisation). Additionally, a precise estimate of plant available nutrients is difficult, since the actual nutrient availability is modulated by biotic interactions (within and across trophic levels, soil fauna etc) and climate which both vary with space and time.

Another, probably equally important, explanation for the relatively low explained variance of the leaf economics traits was provided in Chapter 3 that focused on two important environmental drivers in community ecology: disturbance and nutrient availability. The effects of these two drivers on trait selection have been hypothesized implicitly or explicitly to constrain different suites of traits (Lavorel and Garnier, 2002 and Grime, 2006). In contrast to this hypothesis, I showed that most traits are affected by both drivers, although the relative importance of each driver differs per trait (Chapter 3). This may explain why nitrogen mineralisation and soil C/P in itself cannot fully explain the variation in leaf traits, such as leaf phosphorus content, as also disturbance frequency co-determines this variation. Additionally, Chapter 5 provides evidence that also soil moisture may play a role in determining leaf economics traits (Ordoñez et al., 2010b, Wright et al., 2001), since it was a good indicator of the direction in which SLA and LNC change during succession. Note that also other factors may account for the remaining variability in traits, including historical factors and lag response times of species. Hence, since traits are constrained by multiple environmental drivers, traits may be better predicted from multiple drivers (and traits), in contrast to what has been done in Chapter 4.

Since relationships between environmental drivers and plant traits are currently rather poor (e.g. for nutrients) or even quantitatively unknown (e.g. for water and soil acidity), plant traits may, at least for the time being, be replaced by indicator values. Indicator values, i.e. expert-based numbers, have been designed to reflect the integrated response of

species to specific environmental drivers (Ellenberg et al., 1992, Runhaar et al., 2004). The indicator value system has been criticized because of a circularity of the approach: often indicator values are used to estimate the habitat conditions, which are derived from the indicator values of the vegetation that grows on it (Diekmann, 2003 and references herein). Instead, in Chapter 4 the indicator values were used to reflect the plant response to a measured or modelled environmental driver, analogous to how ‘hard’ plant traits reflect a species’ response to an environmental driver. In addition, Chapter 4 provides evidence that indicator values integrate the various ways a plant can respond to a resource into a single measure. For example, the indicator value for nutrients was better explained by a set of traits (Relative growth rate, LNC, SLA and LPC) than by any of these traits separately (Chapter 4). Although the indicator values perform well in the current climate, their reliability may be questioned once applied to a changing climate. Therefore, I recommend replacing indicator values by functional traits if one aims for a climate versatile model. Ideally, one combines various traits and links these to environmental drivers to attain the same level of predictive power as conventional indicator values.

In this thesis, the trait mean was used as a central measure to distinguish among the plant communities from different environments because in the past years we have got reasonable understanding on how the mean response (net result of convergent and divergent processes) of plant communities can be related to environmental drivers. However, understanding how the environment determines the distribution of trait values (variance, skewness) within communities may provide additional information that can be used to increase the predictive power of a trait-based model. Yet, a first explorative test to use the variance of trait values as an additional variable to distinguish among vegetation types showed the contrary (Chapter 2), probably because different sources of variation (within and between habitats) obscured the predictions. Several studies show that the dispersion of trait-values (variance, second moment) within communities increases with increasing resource availability (water and nutrient availability; Weiher et al., 1998, Cornwell and Ackerly, 2009, Ordonez, 2010). The authors hypothesize that increased resource availability leads to increased competition that, through limiting similarity, leads to dispersion of traits. In addition, Cornwell and Ackerly (2009) showed that the kurtosis (fourth moment) of the trait distribution within communities could be related to the soil moisture status. If these results can be substantiated by more research and translated into predictive relationships, then the distribution of vegetation types can be predicted by the community trait mean and also by other characteristics of the trait distribution, thus potentially increasing the predictive power of a trait-based model.

## **Traits are additionally constrained by other traits**

Trait-trait constraints are at the core of plant ecology and have been used a lot to define the spectrum of plant strategies (Westoby, 1998, Reich et al., 2003). However, whether they also translate to trait-trait constraints at the community level is unknown. The structural equation model (SEM) presented in chapter 3 reveals that at the community

level, besides the constraining effect of environmental drivers on traits, also trait-trait constraints are important. Moreover, I was able to quantify the relative importance of trait-trait constraints vs. environmental constraints and showed that in about half of the traits, trait-trait constraints can explain a larger portion in trait-variation than environmental constraints.

Two processes can account for the trait-trait constraints as found in this study. The first one is that two traits are affected by a common, but unknown, environmental driver. Since this unknown driver is, by definition, not included in the SEM, the common variance is modelled as a trait-trait constraint. For example, both seed mass of the germinule and dispersule may be additionally affected by soil moisture (Ozinga et al., 2004) which was not included in the SEM. The second explanation is that a trait cannot vary without affecting another trait due to physiological and/or morphological constraints. For example, a plant cannot achieve high photosynthesis rate without the photosynthetic enzymes to support this. This kind of causal relationships often lead to tight correlation between traits (Westoby et al., 2002, Reich et al., 2003, Wright et al., 2004) and is for example the case for LNC vs LPC and LNC vs dark respiration (Wright et al., 2004). The other kind of correlation between traits is induced by a non-causal relationship between traits (coordination sensu Reich et al., 2003) and evolves if a particular combination of trait values performs better in a given environment. For example, communities dominated by tall plants also favour plants that produce large seeds (Westoby et al., 2002, Reich et al., 2003). Reich et al. (2003) argue that relationships caused by coordination are often much weaker than causal relationships (and can even be reversed within habitats compared to across habitats). Interestingly, in the SEM, traits indicative of plant size and allometry had a large effect on seed and phenology traits. Since the relationship between the allometry traits and the other two categories of traits is for the most part non-causal, this result suggests that the trait-trait constraints are mainly due coordination between traits.

The occurrence of trait-trait constraints hampers the accurate prediction of individual traits as long as only the effects of environmental drivers are included in a trait-based model. Chapter 3 shows that SEM is a helpful tool from going beyond simple multiple regressions to a more mechanistic understanding of how traits are constrained by both environment and other traits. However, the drawback of this technique is that the trait-trait constraints cannot be easily implemented in a trait-based model since they are not related to the environmental drivers. A solution to this problem is to explicitly model the variation around the environment trait relationship and use the trait-trait constraints to predict the value of the other traits. However, I think that the real way forward is to develop an optimization model that simultaneously optimizes a suite of traits at the level of individuals given multiple environmental constraints, competition and internal physical, physiological and morphological trade-offs (Marks and Lechowicz, 2006). This optimisation model then predicts a number of individuals that have a suite of trait values that is optimal given the environmental constraints and internal trade-offs, which can be used to calculate a community trait mean to predict vegetation types.

## Traits from different strategy axes are needed to optimally describe the floristic variation between plant communities

The traits chosen to be predicted based on environmental drivers and internal constraints should be part of different strategy axes to reflect the various ways in which species cope with the environment (Reich et al., 2003). At the species level, classically, two or three major axes of specialisation are distinguished on which each species has a selected position: a size axis, with maximum canopy height as a dominant representative, a resource acquisition axis with specific leaf area as representative trait (Diaz et al., 2004) and a third axis that represents the ability to disperse and establish (Westoby, 1998, Laughlin et al., 2010). Chapter 2 shows that these axes also describe a great part of the trait variation at the community level. This is not surprising given the fact that the size axis distinguishes communities with intense disturbance from not frequently disturbed habitats (Chapter 3). Maximum canopy height is indicative of the decreasing disturbance frequency and consequently the increased competition for light; the leaf economics traits axis separates fertile habitats in which fast plant growth is needed from unfertile habitats in which resource conservation is required (Chapter 3). These disturbance and resource axes seem to be most important in describing the trait variation among communities (results PCA, Chapters 2 and 3). Nevertheless, the analysis in chapter 2 also clearly revealed that there is more besides these two axes. To optimally describe the functional variation in plant communities, other traits are at least as important. Among these traits are seed mass (as predicted by Westoby, 1998), stem specific density (SSD) and plant life span (LSP). SSD may distinguish vegetation types along a moisture gradient (maximizing hydraulic conductance vs. minimizing the risks of cavitation and/or storage capacity of water in stems, Westoby and Wright 2006, Chave et al., 2009). LSP allows to differentiate among short vegetation types of fertile soils, most notably between ruderal and grasslands communities (similar results were found by Pillar and Sosinski, 2003 and Shipley et al., 2011).

Perhaps the most surprising result is that the predictive power of a set of traits cannot be explained by the extent to which a set of traits is statistically correlated (Chapter 2). In other words, traits maybe strongly correlated but if they come from different strategy axes, their residuals still contain valuable information. Therefore, a combination of functionally different (and not necessarily statistically different) traits is needed to distinguish among communities. For some of these core traits (maxCH, LNC, SLA), we already have identified the most important environmental drivers that constrain those traits, but more research is needed to identify the most important environmental drivers that account for the variation in seed mass, stem specific density and life span.



## The key question: what is the maximum predictive power of a trait-based approach?

Although it is clear that a trait-based approach has several advantages above current approaches, the key question is: what is the maximum predictive power of a trait-based model if the above three critical conditions are fulfilled? Before answering this key question, a fourth factor that affects the predictive power of a trait-based model, the scale at which predictions are made, needs consideration. The most appropriate scale for HDMs is the topic of a difficult and recurrent debate (see Guisan and Thuiller, 2005 dealing with this issue); after all it greatly depends on the purpose of the model and the study area of interest. A first sensible requirement, that is also valid for trait-based HDMs, is that the scale for which the model is developed determines the traits that should be selected - and the environmental drivers considered in relation to this trait. For example, the leaf life span (LLS) of deciduous species has been shown to strongly depend on the length of the growing season (van Ommen Kloeke et al., 2011) and can therefore be used at a global scale. Hence, if used within one climatic region it is probably not the best trait to distinguish among plant species.

Secondly, the accuracy with which the vegetation types can be predicted depends on the number of vegetation types (resolution) that are distinguished within a given trait-space. Chapter 4 shows that considering more detailed distinctions among vegetation types leads to a decrease in the accuracy of the predictions due to an increasing overlap in trait space. This decreased accuracy reflects a fundamental uncertainty, since the likelihood of occurrence for two vegetation types that have the same functional characteristics is equal. Chapter 4 showed that currently about 10-15 vegetation types for a national vegetation model are optimal to balance between resolution and accuracy.

From this perspective it does not seem feasible to predict the occurrence of individual species with sufficient accuracy. Moreover, empirical evidence shows that trait variation within communities is one of the largest sources of trait variability, which needs to be quantified when predicting individual species, but quantitative knowledge on those is currently limited. Additionally, because assembly rules only determine the characteristics of species that can enter the species pool, which of the species with those characteristics becomes part of the community is a random process. These random processes include the order of arrival of species and species-specific interactions. As a result, at small scales species assemblages may seem random (Van der Maarel and Sykes, 1993).

Chapter 4 shows that with the current state of art - using four traits and four environmental drivers and 13 vegetation types - the distribution of vegetation types within the Netherlands can be predicted reasonably accurately; the chance-corrected agreement of the model at the landscape level was 0.74. This performance is comparable - although an exact comparison was not possible (Chapter 4) - to conventional HDMs that did not have traits incorporated. At plot level (10-100 m<sup>2</sup>), a moderate 52% of the plots was correctly assigned to a vegetation type. Part of the explanation for the fact that the site-



specific performance is lower than the landscape performance is that at site level multiple vegetation types have a chance to occur given a specific set of traits. As a result, the observed vegetation type and the vegetation type predicted with the highest probability do not always match. At the landscape level, however, the predicted frequencies and observed frequencies showed much more agreement. Even if the improvements which have been suggested in the previous sections are incorporated in the trait-based model, it cannot be expected that this model - like any model - will perform perfectly because communities are assembled by the combined effect of niche-based processes (Keddy, 1992a) and neutral processes (Hubbell, 2001, Sonnier et al., 2010). The latter part is inherently unpredictable, which makes it impossible to predict the exact composition of a species assemblage. This is something we, and probably policy makers as well, have to acknowledge. Despite this fundamental uncertainty, I think that the reasonably high performance of the current trait-based model opens a window of opportunity to develop this approach further, because it explicates the processes that determine the vegetation distribution.

## Application of trait-based models for future projections

A trait-based modelling approach was followed, as discussed in the previous sections, since we expect that the reliability of the vegetation types predictions under changing environmental conditions may improve by the inclusion of traits. Before applying such approach to future projections, two additional aspects need consideration: 1) the role of climatic extremes in trait selection and 2) the stability of current vegetation types.

It is expected that in the future, weather extremes will occur more frequently (Meehl and Tebaldi, 2004, Meehl et al., 2007). How these weather extremes affect vegetation composition is only partly known, though there is empirical and theoretical evidence that it can greatly affect ecosystem functioning (Knapp et al., 2002, Ciais et al., 2005, Fischlin et al., 2007 and references herein), because the survival of most organisms is determined by extremes and not by averages. Therefore, ideally, a trait-based model would also incorporate the effects of environmental extremes on the vegetation. A trait-based model is expected to be better able to capture these effects since it allows an explicit link between the environmental extreme and traits responding to it. Predicting the effect of extremes on plants requires that both the effects of the frequency and duration of weather extremes on resource availability are estimated as well as how plants respond to this. In this thesis, a first attempt into this direction was implemented by applying the maximum reduction in respiration across a 10 day period (RS, Bartholomeus et al., 2008b, Bartholomeus, 2009) as estimate of oxygen stress (Chapter 4). RS captures the effect of extreme rainfall events and increased temperature (through increased respiration). However, how these extremes act on the selection of traits is unclear. Climatic extremes may restrict the upper or lower limit of viable trait values and consequently trait minima or maxima may be much more informative than the mean response when related to environmental drivers (Cade et al., 1999, Austin, 2007). Future research should aim at

selecting a few core traits that captures the various ways how plants can resist or avoid extremes. For example, resistance to cavitation in case of drought, ability to pump oxygen into the roots in case of waterlogging (e.g. root porosity), and time needed to complete the life cycle (life span, dormancy).

The trait-based model that is developed in this thesis predicts the occurrence probability of vegetation types. However, the reliability of this approach ('assemble first, predict later') can be questioned when the model is applied to a changing climate since it is likely that climate change will modify species interactions and as a result plant communities will change (Ferrier and Guisan, 2006). On the other hand, in the short term, vegetation composition may remain unchanged despite changing environmental conditions, due to acclimation in combination with a lagged response of species to changing environmental conditions (Jump and Penuelas, 2005). As a result, the speed at which vegetation composition will change is unknown and therefore if the current model is applied in a changing climate the predicted vegetation types should not be regarded as exact representations of the future flora, but rather as reference points in a multidimensional trait space. An advantage of our approach is that our model allows predicting new combinations of vegetation types if vegetation types that may arise in the future would be included. This may be done by including for example vegetation types from nearby regions that currently have the projected conditions or by including reconstructed paleo-vegetation types.

## **Towards a dynamic trait-based model**

This thesis presents a static trait-based model, while for future projections, a dynamic model could have additional merits. Some of the traits, most notably those traits that are strongly affected by biogeochemical cycles, can in turn have a large impact on the speed and direction of these cycles. For example, leaf nitrogen can be linked to nitrogen availability in the soil (Ordoñez et al., 2009), but nitrogen availability itself depends on the decomposability of plant tissues which on its turn is affected by the carbon and nitrogen content of the plant tissues (Garnier et al., 2004, Quested et al., 2007, Cornwell et al., 2008, Weedon et al., 2009). As a first step towards a dynamic trait-based model, Chapter 5 explores if and how traits change consistently with succession for a wide range of ecosystems. It shows that traits involved in competition for light shift consistently across ecosystems, while the shift in traits related to soil abiotic conditions, is determined by the initial soil abiotic conditions. As a result, the trajectories of ecosystems through trait space can be explained by a combination of an universal response to changing light availability and a specific response pending on the initial abiotic conditions of that ecosystem.

It is very promising - and it has not been shown before - that trait trajectories are predictable during succession across a wide range of ecosystems. As a result, the consistent and predictable shifts of traits during succession open up a future for dynamic trait-based models. Although I showed that the initial conditions play a big role in determining the direction of the trait changes during succession, the speed of these

changes could not be assessed in my analysis. Therefore, to determine the tempo of trait changes, vegetation-soil feedbacks need to be quantified. These feedbacks—most notably through carbon and nitrogen fluxes—are determined by the traits themselves (Garnier et al., 2004, Quested et al., 2007, Cornwell et al., 2008, Weedon et al., 2009), as well as by the amount of litter that is produced by the vegetation (Aerts, 1999). The amount of litter that is produced depends on the absolute amount of biomass produced, the allocation of biomass over the different plant tissues and the life span of these tissues (Berendse, 1994). The life-span of the tissues can probably be estimated by the amount of nitrogen and secondary compounds in the tissues, which are among others a function of soil fertility (Aerts and Chapin, 2000, Wright et al., 2004, Ordoñez et al., 2009). However, no sound conceptual solution within the trait-based approach exists to estimate the amount of biomass production. Several approaches have been proposed, varying from very simple empirical relationships to mechanistic plant growth models. Among the simple approaches are i) estimates of net primary production as a function of the relative growth rate of the vegetation (which can be a function of soil nutrient and water availability; Lavorel and Garnier, 2002 and Garnier et al., 2004 based on Chapin et al., 1993) and ii) the empirical relationship between the indicator value for nitrogen and standing biomass (Ertsen et al., 1998). Other approaches are based on allocation rules and scaling theory and partition nutrients and biomass among plant parts to predict ecosystem productivity (Kerkhoff et al., 2005, Niklas et al., 2005, Kerkhoff and Enquist, 2006). More complex approaches, though limited in the number of species modelled, use growth models to estimate ecosystem productivity (van Oene et al., 1999, van Wijk, 2007 among others). The latter type of models is most promising in providing estimates of litter production as they integrate the availability of multiple resources to estimate biomass and its distribution among the plant parts. Alternatively, an optimisation model that predicts both an optimal set of traits and biomass may be used to predict ecosystem fluxes and hence feedbacks.

## Conclusions

This thesis shows that a trait-based model can be successfully implemented. Moreover, it shows that a static trait-based approach does not necessarily lead to a low predictive power compared to conventional HDMs. Additionally, this thesis has identified critical success factors that will further increase the performance of a trait-based model. These success factors include: i) predicting traits from multiple environmental drivers, ii) incorporating trait-trait constraints, iii) the use of functionally different traits to predict species assemblages and finally, iv), a balance between the resolution and accuracy. Altogether, this thesis presents a trait-based model as proof of concept along with a number of improvements that can be made to this modelling approach and herewith opens a window of opportunity to develop the trait-based modelling approach further.